A REVISION OF THE BRACHIOPOD FAMILY LEPTOCOELIIDAE

by ARTURO AMOS and A. J. BOUCOT

ABSTRACT. The Leptocoeliidae are redefined to include atrypaceans bearing unbranched plications commonly with a relatively angular cross-section. The common Silurian species *Eocoelia hemisphaerica* differs from the Devonian members of the Leptocoeliidae in not having a cardinal process. True *Leptocoelia* occurs in the Precordillera of San Juan and Mendoza, Argentina, this being the first occurrence of the genus in the Malvinocaffric Province of South America and South Africa where *Australocoelia* (the '*Leptocoelia flabellites*' of most papers on the Lower Devonian of this region) is the common leptocoeliid. *Leptocoelia infrequens* (Walcott 1884) from the Nevada limestone is redescribed. The new species *L. nunezi* from the Lower Devonian of Argentina, *L. nunezi texana* from the Lower Devonian of central Texas and Venezuela, and *E. quebecensis* from the Lower Silurian of Quebec are described. The leptocoeliids display a progressive tendency toward the loss of the dental lamellae in the pedicle valve during the Lower Silurian (Llandovery), followed by the development of complex cardinal processes in the Lower Devonian. Leptocoeliids have not yet been recognized from the Ludlow. The leptocoeliids are known chiefly from the New World during the Lower and Middle Devonian with the exception of *Australocoelia*, which also occurs in South Africa and Tasmania, and of *Leptocoelia*, which also occurs in Kazakhstan.

THE atrypaceans of the Lower Paleozoic are a puzzling group of brachiopods whose internal and external morphology at first appear to be very confused. Restudy of the Leptocoeliidae, which include those atrypaceans having unbranched plications commonly with a relatively angular cross-section, indicates that they can be readily distinguished from the other groups.

At the time Boucot and Gill's paper appeared in 1956, a new Devonian fossil locality was found in the Precordillera of San Juan and Mendoza in western Argentina, by Fernandez (1957) and E. Nuñez about 5 kilometres north-east of Quebrada de la Flecha in the foothills of the Sierra Chica de Zonda. The specimens were found in sediments belonging to the Rinconada formation. New collections and examination by the writers led to the conclusion that they belong to the new species *Leptocoelia nunezi*.

The finding of this brachiopod, together with an unidentified trilobite, in rocks considered heretofore to be of various ages ranging from Ordovician to Devonian ends a long dispute on the age of the Rinconada formation. The problem it raises regarding the distribution and palaeogeography of leptocoeliids in the Malvinocaffric province will be dealt with later on.

While studying numerous collections of Silurian brachiopods from Gaspé and the Eastern Townships of Quebec, Boucot in 1957–8 became aware that the shells commonly assigned to *Coelospira hemisphaerica* were in reality leptocoeliids and that they could be subdivided into two groups on the basis of the presence or absence of dental lamellae. During a visit to Dr. O. I. Nikiforova in Leningrad during the summer of 1960, Boucot found that she had in preparation a paper, since published, in which '*C.*' *hemisphaerica* was assigned to a new genus. Subsequently Mr. Alfred M. Ziegler, Oxford University, has arrived at the same conclusion based on English material. We are greatly indebted to Ziegler for critically reading the manuscript and generously contributing from his knowledge of British Silurian leptocoeliids.

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Both writers are grateful to Dr. G. A. Cooper for permitting use of the facilities and collections of the U.S. National Museum during the preparation of this paper. Boucot is also indebted to Drs. F. F. Osborne, J. Béland, and P. Lesperance of the Quebec Department of Natural Resources for providing the Silurian collections from which the specimens of *Eocoelia* were obtained. We are indebted to Dr. H. Castellaro of the University of Buenos Aires for the loan of specimens of *Australocoelia* from various Argentine localities; also to Dr. J. Fernandez and E. Nuñez of the Geological Survey of Argentina, who discovered and pointed out to the writers the fossil locality which provided *Leptocoelia*. The work by Amos was carried on during the tenure of a Guggenheim Foundation fellowship, for which he expresses his gratitude.

The Canadian material of *Eocoelia* is deposited at the Redpath Museum, McGill University, Montreal; the Argentine material of *Australocoelia* and *Leptocoelia* is deposited at the Cátedra de Paleontología, Facultad de Ciencias Exactas y Naturales, University of Buenos Aires, Argentina (C.P.U.N.B.A.).

Thanks are due to Dr. C. L. Forbes, Assistant Curator, Sedgwick Museum, Cambridge, for providing the excellent stereo-pairs of *Eocoelia hemisphaerica sefinensis*. Boucot's share of the work was supported by N.S.F. contract DSR 8298 to M.I.T.

Finally, we are very grateful to Dr. P. F. Moore, B.P.M., The Hague, for permission to illustrate the Venezuelan specimens of *Leptocoelia nunezi texana* collected by Bowen. The figured Venezuelan specimens have been deposited in the British Museum (Natural History).

SYSTEMATIC DESCRIPTIONS

Superfamily ATRYPACEA
Family LEPTOCOELIIDAE Boucot and Gill 1956, emended

Definition. The family Leptocoeliidae is here redefined to include coarsely and angularly plicate atrypaceans in which the plications increase in size anteriorly. The plications all originate at the beaks of the valves. Included within the family are genera both with and without a cardinal process, and with and without a well-developed fold and sulcus.

Comparison. The Coelospiridae include two groups of genera which may be grouped into the subfamilies Coelospirinae and Anoplothecinae. The Coelospirinae are distinguished from the members of the Leptocoeliidae by the presence of bifurcating plications. The Anoplothecinae are distinguished from the Leptocoeliidae by the presence of very low plications and abundant frilly growth lamellae.

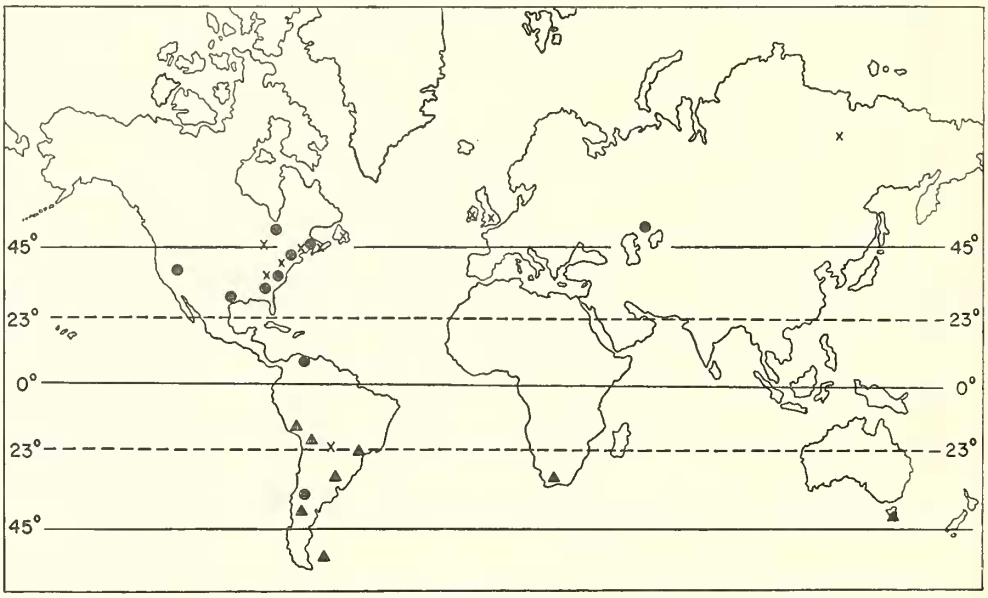
Genera:

Leptocoelia Hall 1857, *10th Ann. Rpt. New York State Cab. Nat. Hist.*, p. 107.
Australocoelia Boucot and Gill 1956, *J. Paleo.* **30**, pp. 1174–5.
Eocoelia Nikiforova 1961, *Paleozoic Biostratigraphy of the Siberian Platform*, part 1, pp. 252–5, pl. liv, figs. 8–16, text-fig. 45.

Distribution. Leptocoelia, which previously has been unreported from outside of North America (where it is known from Gaspé in the east to Nevada in the west), is now known from the Malvinocaffric Province (Table 1, text-fig. 1), where it occurs in the Precordillera of San Juan and Mendoza in Argentina. *Leptocoelia* is now known also to occur in Venezuela and in Kazakhstan (Dr. M. Rzonsnitskaya kindly showed Boucot a

TABLE 1. Distribution of the Leptocoeliidae

Australocoelia	*Leptocoelia*	*Eocoelia*	*Genera*
	×	×	Northern Appalachians (including Nova Scotia)
	×	×	Central and South Appalachians
	×	×	Mid-Continent and West
×			Brazil (south of the Amazon)
×		×	Paraguay
×			Peru
×			Uruguay
×			Bolivia
	×		Venezuela
×	×		Argentina
×			Falkland Islands
×			South Africa
×			Tasmania
		×	Europe
		×	Siberia
	×		Kazakhstan
		×	Australia



TEXT-FIG. 1. Distribution of the Leptocoeliidae. Circles represent occurrences of *Leptocoelia*, triangles represent occurrences of *Australocoelia*, and ×'s represent occurrences of *Eocoelia*.

specimen whose cardinalia and external form leave no doubt as to its assignment to *Leptocoelia;* Sarycheva 1960, p. 264). *Australocoelia* is still known only from the Malvinocaffric Province (the southern two-thirds of South America and South Africa), and from Tasmania, as previously reported by Boucot and Gill (1956). *Eocoelia* is known from the Llandovery of western Europe, eastern North America, Paraguay, Australia and Siberia, and has been recognized in strata of Wenlock age in the northern

Appalachians and England. The absence of leptocoeliids of Ludlow age is puzzling, but may be understandable if the absence of post-Wenlock leptocoeliids from Europe is considered together with the fact that the Ludlow brachiopod faunas of North America have been little studied; furthermore, Ludlow beds have not yet been recognized in South America or South Africa, where Lower Devonian leptocoeliids are known.

The absence of leptocoeliids from the Devonian of the Old World (except for Asiatic Russia) can probably be explained by considering that *Anoplotheca*, whose form and size are similar to that of *Leptocoelia* and *Australocoelia*, may have filled the ecologic niche occupied elsewhere by the latter two genera.

Evolutionary trends. Eocoelia quebecensis and *E. paraguayensis* have short dental lamellae in the pedicle valve and are the oldest members of the Leptocoeliidae (known from strata of Llandovery age). By about the middle of the Upper Llandovery (C_3 time) dental lamellae are no longer present in large specimens of the genus, as represented by *E. hemisphaerica*. Shells of the *E. hemisphaerica* type are known until Wenlock time and, in common with the earlier species, lack a cardinal process in the brachial valve. There is no record of the Leptocoeliidae in strata of Ludlow age. By about Upper Gedinnian time (New Scotland formation time) Leptocoeliidae, lacking dental lamellae (as do the younger forms of *Eocoelia*) but possessing a complex cardinal process, are known in the northern Appalachians. Leptocoeliidae possessing several types of complex cardinal process persist throughout the remainder of the Lower Devonian and into Lower Eifelian equivalents. *E. paraguayensis* is associated with Lower Llandovery graptolites.

From the above, it can be concluded that the Leptocoeliidae show a progressive tendency toward the reduction of the dental lamellae of the pedicle valve, followed by the proliferation of forms with a complex cardinal process. It is here suggested that *Australocoelia* was derived from *Leptocoelia* by further elaboration and complication of the cardinal process. When the cardinal processes of both genera are compared, it is evident that both are built in the same manner, and that, by elevation of the sessile 'trilobed' process above the level of the crural plates on a shaft, an australocoeliid type is developed.

The pre-Llandovery progenitor of the Leptocoeliidae is unknown. However, blocks of Ordovician quartzite from a fault zone in Nova Scotia (Boucot, Griffin, and Fletcher 1959, p. 1572) have yielded an atrypacean with internal characters similar to those of *E. quebecensis*. Unfortunately the Nova Scotia material is too poorly preserved to be definitely assigned generically.

EOCOELIA Nikiforova 1961

Plate 62, figs. 1–16; Plate 64, figs. 12–15; Plate 65, figs. 1–2, 12–17

Type species. Atrypa hemisphaerica J. de C. Sowerby 1839, in Murchison, *Silurian System*, vol. ii, p. 637, pl. 20, fig. 7.

Diagnosis. Eocoelia is characterized externally by a flat brachial valve and convex pedicle valve. Internally *Eocoelia* is characterized by discrete crural plates in the brachial valve.

Comparison. Eocoelia may be distinguished externally from both *Leptocoelia* and *Australocoelia* by the absence of a well-developed fold and sulcus. Internally *Eocoelia*

possesses discrete crural plates, whereas both *Australocoelia* and *Leptocoelia* have a well-developed cardinal process in addition to fused crural plates. The interior of the pedicle valve of the earlier Llandovery species of *Eocoelia* has short, thin dental lamellae, but the later Upper Llandovery species of the genus lack dental lamellae, as do *Leptocoelia* and *Australocoelia*.

EXPLANATION OF PLATE 62

The following institutional names referred to in the descriptions of Plates are abbreviated as follows:

B.M.N.H. (British Museum of Natural History).
C.P.U.N.B.A. (Cátedra de Paleontología, University of Buenos Aires).
P.R.M. (Peter Redpath Museum, Montreal).
U.S.N.M. (U.S. National Museum).

Figs. 1–4. *Eocoelia quebecensis* sp. nov. Point-aux-Trembles formation. Lesperance's 1959 locality No. 59–397 (F), 300 feet north-east and 4,500 feet south-east of the west corner of Lot 42, Range I, Asselin township, Rimouski Co., Quebec. 1, Impression of interior of brachial valve (×2). P.R.M. No. 10061. Holotype. 2, Rubber replica of interior of brachial valve (×4). Note the absence of a cardinal process. P.R.M. No. 10061. Holotype. 3, Impression of interior of pedicle valve (×2). Note the short dental lamellae. P.R.M. No. 10062. 4, Rubber replica of interior of pedicle valve (×2). P.R.M. No. 10062.

Figs. 5–10. *Eocoelia quebecensis* sp. nov. Point-aux-Trembles formation. Lesperance's 1959 locality No. 59–373M(F): '100 feet north-east and 1,800 feet south-east from the west corner of Lot 14, Range I, Asselin township, Rimouski County, Quebec. The outcrop is in the ditch, on the north-east side of a lumber and portage road. This outcrop is found between the intersection of two lumber roads, approximately 400 feet apart, which connect with the lumber road and portage road on which the outcrop is. The fossiliferous outcrop is the south-easternmost of a series of outcrops between these two connecting roads.' 5, Rubber replica of interior of brachial valve (×4). P.R.M. No. 10065. Note the absence of a cardinal process. 6, Rubber replica of exterior of pedicle valve. (×2). P.R.M. No. 10066. 7, Impression of interior of brachial valve (×2). P.R.M. No. 10065. 8, Impression of interior of pedicle valve (×2). P.R.M. No. 10063. Note the short dental lamellae. 9, Rubber replica of interior of pedicle valve (×2). P.R.M. No. 10066. 10, Impression of interior of pedicle valve (×2). P.R.M. No. 10064. Note the short dental lamellae.

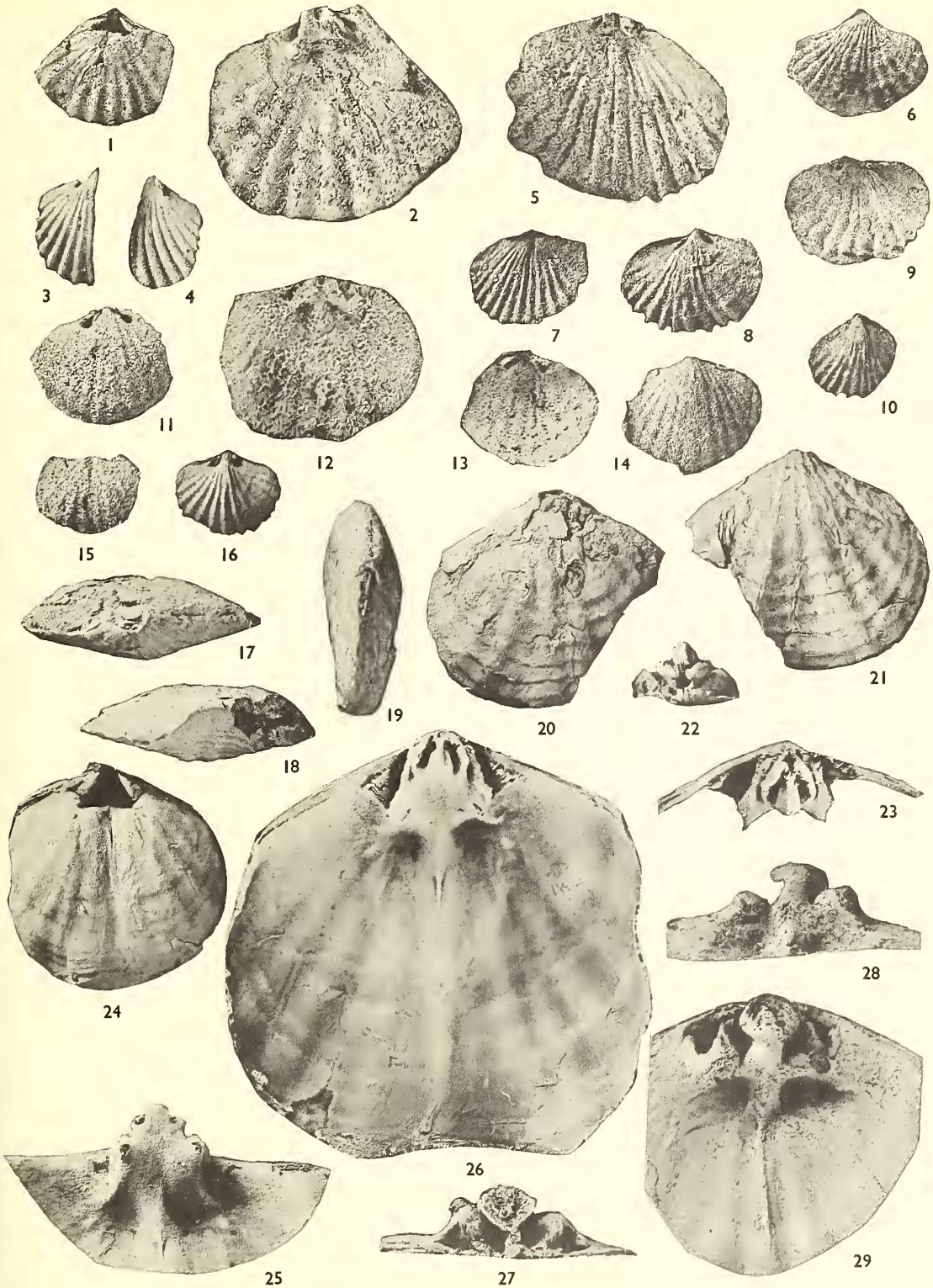
Figs. 11–15. *Eocoelia hemisphaerica* (J. de C. Sowerby). Val Brillant quartzite. Béland's 1959 locality L-53. South-east end of lot 40, Range VI, Fleurido Twp., Matapedia Co., Quebec, 4½ miles due south of village of Ste-Angèle. 11. Impression of interior of pedicle valve (×2). P.R.M. No. 10067. Note the impression of the fossettes and the absence of dental lamellae. 12, Rubber replica of interior of brachial valve (×4). P.R.M. No. 10068. Note the absence of a cardinal process. 13, Rubber replica of interior of pedicle valve (×2). P.R.M. No. 10067. 14, Rubber replica of exterior of pedicle valve (×2). P.R.M. No. 10069. Note the rounded plications. 15, Impression of interior of brachial valve (×2). P.R.M. No. 10068.

Fig. 16. *Eocoelia hemisphaerica* (J. de C. Sowerby). Awantjish shale. Béland's 1959 locality No. AA-12-1. Near boundary dividing lots 8 and 9 at north-west end of lots, Range IV, Awantjish Twp., Matapedia Co., Quebec. 5½ miles south-west of village of St. Cléophas. Impression of interior of pedicle valve (×2). P.R.M. No. 10070. Note the fossettes and the absence of dental lamellae.

Figs. 17–21. *Leptocoelia nunezi* sp. nov. Cerro Bola, San Juan, Argentina. 17, Posterior view. 18, Anterior commissure. 19, Lateral view of holotype. 20, Brachial exterior. 21, Pedicle exterior. (All ×2.) C.P.U.N.B.A. No. 7773a.

Figs. 22–26. *Leptocoelia nunezi* sp. nov. Cerro Bola, San Juan, Argentina. 22, Posterior view of cardinal process (×4). 23, Posteroventral view of cardinal process (×4). 24, Internal impression of brachial valve (×2). 25, Anterior view of cardinal process (×4). 26, rubber cast of specimen in fig. 24 (×4). C.P.U.N.B.A. No. 7775.

Figs. 27–29. *Australocoelia tourteloti* Boucot and Gill. Comarapa–Tunal area, Bolivia. 27, Cardinal process, posterior view. 28, Anterior view. 29, Pedicle view. (All ×4.) Topotype, U.S.N.M. No. 125285.



AMOS and BOUCOT, Leptocoeliidae

Description. Exterior: the brachial valve is flat and the pedicle valve is evenly convex. The hinge line is short and curves anteriorly. The anterior commissure is strongly crenulate. Both valves are ornamented by unbranched plications.

Interior of brachial valve: the cardinalia consist of discrete crural plates laterally flanking the notothyrial cavity, which is partly filled with secondary material to form a notothyrial platform. Immediately anterior of the notothyrial platform is the adductor field, which consists of a low, rounded median septum on either side of which are elongate adductor impressions.

Interior of pedicle valve: hinge teeth are short and stout; thin dental lamellae, if present, border the poorly impressed muscle field. The posterior portion of the delthyrial cavity bears the impression of the pedicle callist. The median face of the hinge tooth, or the dental lamellae if present, is indented (hereafter this groove will be termed a 'fossette', following Cooper 1956) to receive the lateral edge of the crural plate.

Stratigraphic range. In western Europe, *Eocoelia* appears to be restricted to the Upper Llandovery (Williams 1951, p. 129) and its stratigraphic equivalents and the Wenlock of Tortworth (where A. M. Ziegler informs me that Dr. M. Curtis, Bristol, has found the genus in strata of Wenlock age). In western Europe, forms with hinge teeth, but no dental lamellae, are known from both C_4 (Williams 1951, p. 129) and the Wenlock, and with dental lamellae from C_1. In eastern North America, the genus has been recognized in the Appalachians from Alabama (Butts 1926, p. 43, fig. 8) to Newfoundland (Shrock and Twenhofel 1939, p. 262) in strata which the writers consider to be of C_1 to Wenlock age. The North American occurrences of C_1 age are in the Pointe-aux-Trembles formation (Lesperance 1959, oral communication), where a *Stricklandia* similar to *S. lens progressa* Williams, 1951 is associated with a form having short dental lamellae. The occurrences of C_6 to Wenlock age in North America are from the Val Brillant quartzite (which contains *S. gaspeensis* together with forms lacking dental lamellae), and the Chesuncook limestone (which contains *Rhipidium*), and the Long Reach formation of coastal New Brunswick. The North American occurrences of late Upper Llandovery age are in the Clinton group (Gillette 1947, p. 20) and its equivalents from eastern Quebec to New York to Alabama; these Clinton forms have no dental lamellae. *E. paraguayensis*, which is associated with Lower Llandovery graptolites, may be the Lower Llandovery precursor of the Upper Llandovery eocoeliids of the Northern Hemisphere.

Species:

Atrypa hemisphaerica Sowerby, 1839, op. cit.

Coelospira sulcata Prouty, 1923, *Md. Geol. Surv., Silurian*, p. 446, pl. 27, figs. 6–8.

Atrypina? paraguayensis Harrington, 1950, *Contrib. Cient. Fac. Cien. Exac. y Nat.*, t. i, p. 62, pl. i, figs. 9, 10, 13–16. *Coelospira?* cf. *hemisphaerica* (Sowerby) Wolfart, 1961, *Geol. Jahrb.*, p. 65, pl. 2, figs. 8–11.

Coelospira hemisphaerica sefinensis Williams, 1951, *Quart. Jour. Geol. Soc. London*, **107**, pp. 113–14, pl. v, figs. 19–20.

Eocoelia quebecensis sp. nov.

Eocoelia hemisphaerica (J. de C. Sowerby 1839)

Plate 62, figs. 11–16

Atrypa hemisphaerica J. de C. Sowerby 1839, op. cit.

Atrypa? hemisphaerica J. de C. Sowerby, Davidson 1867, *British Silurian Brachiopods*, pt. vii, no. ii, p. 136–40, pl. xiii, figs. 23–30.

Coelospira hemisphaerica (J. de C. Sowerby), Cooper in Shimer and Shrock, *Index Fossils of North America*, p. 319, pl. 121, figs, 22–25.

Coelospira hemisphaerica (J. de C. Sowerby), Shrock, and Twenhofel, 1939, *J. Paleontology*, vol. 13, no. 3, pp. 241–66.

Coelospira hemisphaerica (J. de C. Sowerby), McLearn 1924, *Canada Geol. Survey Mem.* 137, pp. 90–91, pl. x, figs. 20–21.

Atrypa hemisphaerica (J. de C. Sowerby), Billings *in* Logan 1863, *Geology of Canada*, p. 318, fig. 337 *a-b*.

Description: Exterior: the brachial valve is flat and the pedicle valve is almost hemispherical, as suggested by the specific name. Both valves are subcircular in outline. Both valves bear about twelve to eighteen plications, which are separated from each other by narrow interspaces. A weak fold and sulcus may be present. The greatest width of each valve is near the midlength. The hingeline is short. The interareas of both valves are very short. Concentric growth lines are present on both valves. The anterior commissure is crenulate and may be weakly sulcate.

Interior of brachial valve: the cardinalia consist of discrete crural plates laterally bounding the notothyrial cavity, which has been partially filled with secondary material to form a notothyrial platform. The crural plates diverge at an angle of about 45° from the midline, and are relatively blade-like. The crural plates form the antero-median margins of the antero-laterally directed, medially converging, uncrenulated dental sockets. Originating at the base of the notothyrial platform is a low, rounded median ridge that bisects the adductor field and extends anteriorly to about midlength. The adductor impressions are relatively narrow, well impressed posteriorly into a deposit of secondary material, and poorly impressed toward the midlength of the valve. The periphery of the valve is strongly crenulated by the impression of the external ornamentation, but the umbonal region is relatively smooth due to the deposition of secondary material.

Interior of pedicle valve: stout hinge teeth possessing a triangular cross-section lie on either side of the delthyrial cavity. The apex of the triangular cross-section is directed postero-medially. The medial face of each tooth bears a fossette. The posterior portion of the delthyrial cavity bears the impression of the pedicle callist. The muscle field is poorly impressed. The interior is strongly crenulated by the impression of the external ornamentation.

Type. A holotype is not designated due to ignorance of the condition of Sowerby's material. However, Alfred Ziegler informs us that the type specimen in the Geological Survey Museum, London, is labelled 'Caradoc Sandstone of Ankerdine Hill, Worcestershire' and '. . . contains a variety of *E. hemisphaerica* which is closely similar to *E. hemisphaerica sefinensis*. . . '. In view of Ziegler's observations it is probable that the *E. hemisphaerica* of most North American localities may be a new subspecies. We are not setting up such a new subspecies, however, as Ziegler is currently engaged in a thorough study of all the forms belonging to *Eocoelia*.

Stratigraphic distribution. In western Europe *E. hemisphaerica* is restricted to the Upper Llandovery and the Wenlock. *E. hemisphaerica* is reported from strata of Upper Llandovery age in Siberia (Nikiforova 1955, p. 80; 1961, p. 253). In the central and southern Appalachians from New York to Alabama the species is restricted to the

upper portion of the Upper Llandovery (Gillette 1947, op. cit.), but in the northern Appalachians in addition to occurrences as low as C_4 equivalents, the species has been found in the strata of C_6 to Wenlock age in eastern Quebec and southern New Brunswick. The Quebec and New Brunswick occurrences have not previously been noted and are in the Val Brillant quartzite of the Matapedia Valley region and the Long Reach formation respectively. Both the Val Brillant quartzite and the Long Reach formation have yielded *Stricklandia gaspeensis*, which indicates a C_6 to Wenlock age. Kiaer (1908, p. 589) reports '*Leptocoelia hemisphaerica*' from 6a and 6b of the Oslo region, but this citation is still unconfirmed by either a description of the morphology or figures.

Eocoelia quebecensis sp. nov.

Plate 62, figs. 1–10

Diagnosis. E. quebecensis is characterized by the presence of short dental lamellae and about twelve to fourteen angular plications on each valve.

Description. Exterior: the brachial valve is flat and the pedicle valve is almost hemispherical. Both valves are subcircular in outline and bear about twelve to fourteen angular plications which are separated from each other by angular interspaces. The greatest width of each valve is near the midlength. The hinge-line is short and is curved in an anterior direction. The interareas of both valves are very short. The anterior margin is crenulate. Both valves bear concentric growth-lines.

Interior of brachial valve: the cardinalia consist of crural plates laterally bounding the notothyrial cavity, which has been partially filled with secondary material to form a notothyrial platform. The crural plates diverge at an angle of about 45° from the midline and are relatively blade-like. The crural plates form the antero-laterally directed, medially converging, uncrenulated dental sockets. Originating at the base of the notothyrial platform is a low, rounded median ridge that bisects the adductor field and extends anteriorly about one-third the length of the valve. The paired, narrow adductor impressions are discernible only adjacent to the notothyrial platform. The impression of the external ornamentation is noticeable almost into the notothyrial cavity.

Interior of pedicle valve: relatively small hinge teeth basally supported by short, thin dental lamellae border the delthyrial cavity. The dental lamellae diverge from the midline at an angle of about 45°. The short dental lamellae bear a shallow fossette on their medial faces. The muscle field and pedicle callist are very poorly impressed. The interior is crenulated by the impression of the external ornamentation.

Type. The specimen P.R.M. 10061, figured on Plate 62, fig. 1 is here designated as the holotype.

Comparison. E. quebecensis is similar to *E. sefinensis*, but the latter bears fewer plications than the former. The muscle field in the brachial valve of *E. hemisphaerica* and the pedicle callist in the pedicle valve are more deeply impressed than are the corresponding areas in *E. quebecensis. E. quebecensis* is externally almost identical in form with *E. hemisphaerica*, but the former appears to possess more prominent and more numerous concentric growth-lines than the latter.

Stratigraphic distribution. *E. quebecensis* has been recognized only in the Pointe-aux-Trembles formation of the Lake Temiscouata–Lake Touladi region of eastern Quebec. The Pointe-aux-Trembles formation contains a *Stricklandia* similar to *S. lens progressa*, because of which it has been correlated with C_1 of the British Upper Llandovery. Underlying the Pointe-aux-Trembles formation is the Cabano formation, which contains a fauna of Lower Llandovery age in its upper part. Overlying the Pointe-aux-Trembles formation are strata of probable Lower Ludlow age.

The specific identity of the leptocoeliids from the Oslo region (Kaier 1908, p. 589) is questionable, and their occurrence in strata of Lower Llandovery age (6a and 6b) leaves open the possibility that they may be ancestral to *E. quebecensis*.

Eocoelia paraguayensis (Harrington 1950)

Plate 64, figs. 12–15; Plate 65, figs. 1–2

Atrypina? paraguayensis Harrington 1960, *Contrib. Cient. Fac. Cien. Exac. y Nat.*, t. i, p. 62, pl. i, figs. 9–10, 13–16.

Coelospira? cf. *hemisphaerica* Sowerby 1839, Wolfart 1961, *Geol. Jahrb.* p. 65, pl. 2, figs. 8–11.

Description. Exterior: ventral valve is convex, and the brachial is flat to slightly convex. Shape subcircular, somewhat wider than long, with rounded cardinal extremities. Both valves bear fifteen rounded plications separated from each other by smaller and rounded interspaces. The mesial plicae are slightly wider than the rest, and the two near the extremities are poorly marked. Growth-lines not well developed.

Interior of brachial valve: short divergent crural plates bound the notothyrial cavity. Low rounded median ridge extending anteriorly to about midlength.

Interior of pedicle valve: stout hinge teeth diverging at an angle of 110°. Muscle impressions poorly developed. Dental lamellae poorly developed, if at all.

Holotype. C.P.U.N.B.A. 636 (figured in pl. i, fig. 10, Harrington 1950). Dimensions: length 7·5 mm.; width 7·0 mm.

Observations. Wolfart (1961) has recently added more information on the interior of this Paraguayan species. He states that the pedicle valve has short dental lamellae of about 1·5 mm. diverging about 100° to 130°. Regarding the brachial valve he states that 'Der

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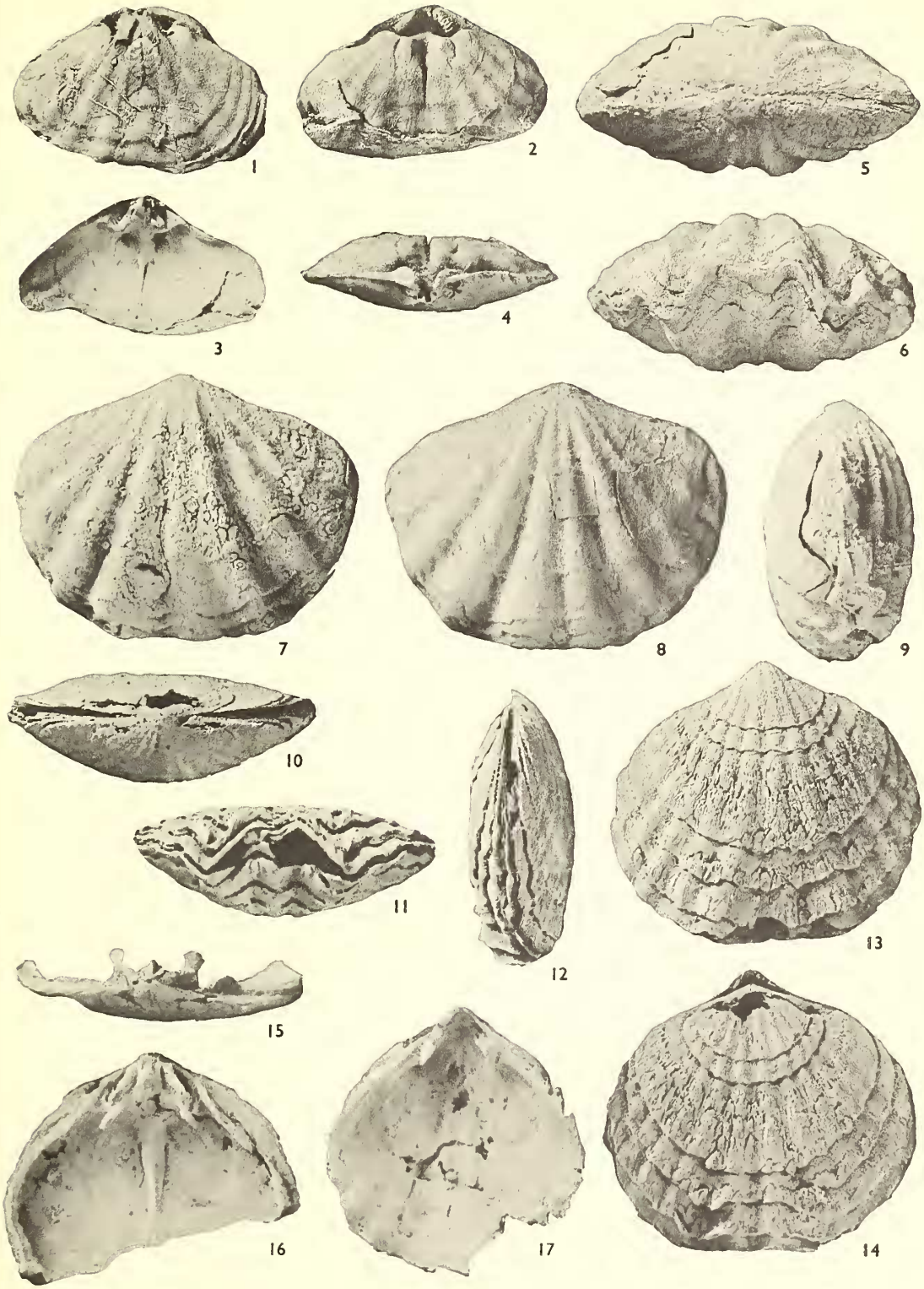
EXPLANATION OF PLATE 63

Figs. 1–4. *Leptocoelia munezi* sp. nov. Cerro Bola, San Juan, Argentina. 1, Internal impression of pedicle valve. 2, Internal impression of brachial valve. 3, Rubber cast of specimen in Fig. 1. 4, Posterior view. (All ×2.) C.P.U.N.B.A. No. 7774.

Figs. 5–9. *Leptocoelia infrequens* (Walcott). Eureka District, Nevada, U.S.A. 5, Posterior view. 6, Anterior commissure. 7, Exterior of pedicle valve. 8, Exterior of brachial valve. 9, Lateral view. (All ×3.) U.S.N.M. No. 13843.

Figs. 10–14. *Leptocoelia munezi texana* subsp. nov. Johnson City, Texas, U.S.A. 10, Posterior view, 11, Anterior commissure. 12, Lateral view of holotype. 13, Pedicle exterior. 14, Brachial exterior. (All ×3.) U.S.N.M. No. 138777.

Figs. 15–17. *Leptocoelia munezi texana* subsp. nov. Johnson City, Texas, U.S.A. 15, Posterior view of cardinal process, U.S.N.M. No. 138779. 16, Brachial interior of same specimen. 17, Pedicle interior. U.S.N.M. No. 138778. (All ×3.)



AMOS and BOUCOT, Leptocoeliidae

zweiteilige Schlossfortsatz und das Medianseptum sind nur andeutungsweise vorhanden'.

The wider mesial plicae of this species is the most conspicuous differential character.

E. paraguayensis occurs in the Lower Llandovery formations of Paraguay (Piribebuy sandstones of Harrington 1950; Eusebio Ayala Sandstones of Wolfart 1961) together with *Calymene boettneri* Harrington. Also graptolites occur which were described by Turner (1959) as *Climacograptus innotatus brasiliensis* Ruedeman and *Diplograptus modestus* Lapworth.

Genus LEPTOCOELIA Hall 1859
Leptocoelia infrequens (Walcott 1884)

Plate 63, figs. 5–9

Trematospira? infrequens Walcott 1884, Monograph VIII, *U.S. Geol. Survey*, p. 151, pl. 4, fig. 3 *a–b*.

Description. Exterior: transverse subpentagonal in outline, maximum width anterior to hinge-line. Uniformly biconvex, greatest thickness at midlength. Pedicle umbo slightly incurved over brachial. Surface covered with eight coarse subrounded plications, separated by deep interspaces. Broad and not very deep sulcus with mesial plication smaller in size than lateral. Growth lamellae conspicuous anteriorly. Brachial valve with inconspicuous umbo, surface with six coarse plications similar to those on pedicle. Fold with deep narrow median groove giving the appearance of two plications. Growth lamellae as in the pedicle valve.

Interior of brachial valve: cardinal process directed ventrally, mesial ridge high. Crural plates slightly divergent. Other characters unknown.

Interior of pedicle valve: unknown.

Dimensions (in mm.).

	U.S.N.M. 13843	U.S.N.M. 138837a
Width	18·2	16·3
Length	14·2	12·5
Thickness	8·4	7·2
Width of sulcus	8·6	7·4
Depth of sulcus	3·3	4·0

Horizon. Lower *Spirifer pinyonensis* zone.

Holotype. Lone Mtn., 18 miles north-west of Eureka, Eureka Dist., Nevada. Unfigured specimen: west side of Lone Mtn., 18 miles north-west of Eureka, Eureka Dist., Nevada.

Comparison. Cooper (in Boucot and Gill, 1956) pointed out that *Trematospira? infrequens* Walcott was a leptocoeliid. Excavation of the interior by Boucot has shown that it belongs to *Leptocoelia;* the cardinal process is of the type shown in the Argentine species *L. nunezi* sp. nov. *L. infrequens* (Walcott) is readily separated from the type and other described species by its subpentagonal transverse outline.

In other specimens from Lone Mountain in the Eureka District (saddle in west side) the fold seems to be well elevated from the flanks and not so transverse (U.S.N.M. 138835).

Leptocoelia munezi sp. nov.

Plate 62, figs. 17–26; Plate 63, figs. 1–4, 10–17; Plate 64, figs. 1–7; Plate 65, figs. 5–6, 10–11

Diagnosis. Coarsely plicate biconvex *Leptocoelia* with cardinal process directed ventrally.

Description. Exterior: subcircular in outline, slightly wider than long, maximum thickness at one-third the length of the shell, maximum width at midlength. Pedicle valve sulcate, convex posteriorly, less so anteriorly. Umbo small, apparently not incurved over hinge-line. Surface covered with eight coarse plications, the two bounding the sulcus broader. Sulcus not very deep, about two-thirds the thickness, width about one-half that of the shell; mesial plicae on sulcus narrower in width. Brachial valve slightly more convex than pedicle and shorter, covered with six, possibly eight, coarse plications; fold with shallow mesial sulcus. Surface of both valves covered with widely spaced growth lamellae.

Interior of brachial valve: 'Trilobed' sessile cardinal process directed ventrally with blade-like median ridge, lateral ridges high, posteriorly curved toward the central lobe. Crural plates slightly divergent buttressing and parallel to cardinal process. Sockets deep, trigonal, and transversely striated. Median ridge high posteriorly extending from base of cardinal process to about one-half the length of the valve and tapering anteriorly. Posterior adductors oval and small, surrounded by a curved short low ridge; anterior pair larger and somewhat longer than median ridge. Pinnate pallial sinuses, with five pallial trunks on each side of valve, trunks branching just before the anterior margin.

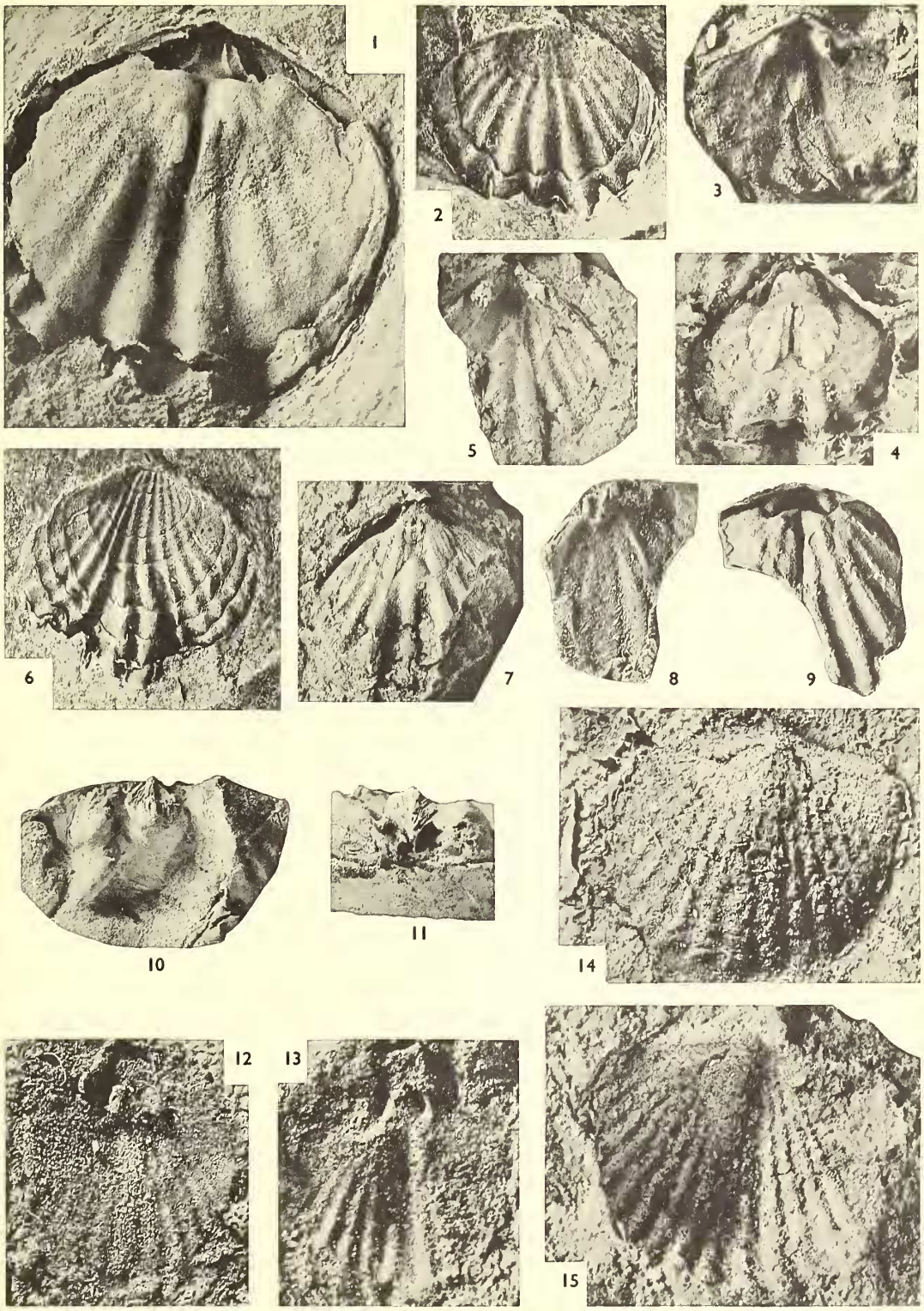
EXPLANATION OF PLATE 64

Figs. 1–7. *Leptocoelia munezi texana* Amos and Boucot, sp. nov. Perija, Venezuela. Collected by J. M. Bowen, Shell Oil Company. 1, Impression of interior of brachial valve (×4). Note the median slit occupied by the ridge on the cardinal process. Nr. Bow. 3489, Quebrada Macaurel; Cano del Oeste formation. B.M.N.H. no. BB. 48088 a and b. 2, Impression of exterior of brachial valve (×2). Nr. Bow. 3489, Quebrada Macaurel; Cano del Oeste formation. B.M.N.H. No. BB. 48089. 3, Rubber replica of interior of pedicle valve (×2). Nr. Bow. 3314 Cano del Oeste. Cano del Oeste formation. B.N.M.H. No. BB. 48092. 4, Rubber replica of exterior of pedicle valve (×3). Nr. Bow. 3732, Cano Colorado; Cano del Oeste formation. B.M.N.H. No. BB. 48093. 5, Rubber replica of interior of pedicle valve (×2). Nr. Bow. 3248. Cano Grande; Cano del Oeste formation. B.M.N.H. No. BB. 48090. 6, Impression of exterior of pedicle valve (×2). Nr. Bow. 3248. Cano Grande; Cano del Oeste formation. B.M.N.H. No. BB. 48091. 7, Impression of interior of pedicle valve (×2). Nr. Bow. 3248. Cano Grande; Cano del Oeste formation. B.M.N.H. No. BB. 48091. 7, Impression of interior of pedicle valve (×2). Note the flabellate diductor impression expanding laterally and the medially enclosed adductor pits. Nr. Bow. 3248, Cano Grande; Cano del Oeste formation. B.M.N.H. No. BB. 48090.

Figs. 8–9. *Leptocoelia? sp.* Cerro Agua Negra, San Juan, Argentina. 8, Rubber cast. 9, Internal impression of brachial valve of same specimen. (Both ×3.) C.P.U.N.B.A. No. 7778.

Figs. 10–11. *Australocoelia tourteloti* Boucot and Gill. Loma de Los Piojos, San Juan, Argentina. 10, Interior of brachial valve showing cardinal process (part of the pedicle valve has been scraped off). 11, Posterior view of cardinal process of same specimen. (Both ×4.) C.P.U.N.B.A. No. 7780a.

Figs. 12–15. *Eocoelia paraguayensis* (Harrington, 1950). Pirebebuy sandstone, Paraguay. 12, Rubber replica of interior of brachial valve (×5). C.P.U.N.B.A. No. 632. 13, Impresssion of interior of brachial valve (×5). Same specimen illustrated in fig. 12. 14, Rubber replica of exterior of pedicle valve (×5). C.P.U.N.B.A. No. 653. 15, Impression of exterior of pedicle valve (×5). Same specimen illustrated in fig. 14.



AMOS and BOUCOT, Leptocoeliidae

Interior of pedicle valve: strong divergent teeth, transversely striated. Muscle impression circular, divided by faint low myophragm.

Dimensions:

	Holotype C.P.U.N.B.A. 7773a	C.P.U.N.B.A. 7775
Width	20·8	18·6
Length	17·2	18·3
Thickness	6·2	..
Depth of sulcus	4·0	4·0
Width of sulcus	9·6	10·2

Horizon and locality. Rinconada formation, Lower Devonian. Cerro Bola, headwaters of Quebrada norte, 5 km. north-east of Quebrada de la Flecha, west of Canada Honda Station, San Juan, Argentina.

Comparison. Leptocoelia nunezi sp. nov. differs from *L. flabellites* (Conrad) in being biconvex, and in having fewer and coarser plications in both valves. Comparison was made with specimens of *L. flabellites* (Conrad) from the Glenerie limestone of New York (U.S.N.M. 125183).

L. nunezi differs from *L. infrequens* (Walcott) in being subcircular and in the lower convexity of their valves.

A specimen (C.P.U.N.B.A. 7778) from Cerro Agua Negra (south-east of Jachal), Argentina. (Pl. 64, figs. 8–9), shows an internal impression of a brachial valve which apparently has the *Leptocoelia* type of cardinal process. Unfortunately preservation does not allow a definite generic identification. *Australocoelia tourteloti* Boucot and Gill also occurs in this locality.

Leptocoelia nunezi texana, subsp. nov.

Plate 63, figs. 10–17; Plate 64, figs. 1–7; Plate 65, figs. 5–6, 10–11

Leptocoelia aff. *L. flabellites* (Conrad), Barnes and Cloud 1947, p. 132

Diagnosis. Circular to subpentagonal *Leptocoelia* with cardinal process directed posteriorly.

Description. Biconvex, circular to subpentagonal in outline, maximum width and thickness at midlength. Pedicle valve sulcate, uniformly convex. Umbo small, pointed, very slightly incurved over brachial umbo. Surface covered with ten to twelve coarse plications, those near posterolateral margins obsolete. Sulcus shallow, about one-half the shell width; depth one-half the thickness; mesial plicae as wide as lateral bounding ones. Brachial valve slightly shorter and somewhat flatter than pedicle, with eight to ten plications; fold with narrow mesial furrow. Surface of both valves covered with widely spaced growth lamellae.

Interior of brachial valve: 'Trilobed' cardinal process with high central ridge and low lateral ridges. Crural plates high, divergent, buttressing cardinal process. Sockets deep and divergent. Median ridge high and broad posteriorly, tapering anteriorly, extending about one-half the length of the valve. Muscle impressions not distinct.

Interior of pedicle valve: elongated blade-like, strong teeth. Elongated and small heart-shaped muscle impression divided by thin myophragm.